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博 士 学 位 论 文

水稻多蘖矮秆突变体的基因精细定位  
与蛋白质组学研究

**Fine Mapping and Proteomics Analysis of a  
High-tillering Dwarf Mutant in Rice**

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## 摘要

水稻是世界上最重要的粮食作物之一,分蘖和株高是其株型结构中最重要两个农艺性状。本研究对籼型多蘖矮秆突变体“佳禾丛矮”(JHCA)进行遗传分析,表明它同时携带互不等位的半矮秆基因 *sd1* 和另一个由核基因隐性突变造成的多蘖矮秆基因,命名为 *xmd(t)*。从 JHCA 与野生型高秆品种“广场 13”(GC13)的杂交后代中分离出只带 *xmd(t)*的单基因突变型品系,经多代自交,达到遗传稳定,命名为“新佳丛”(XJC)。通过分子标记的连锁分析,将 *xmd(t)*基因精细定位于第 1 号染色体上由两个 SSR 分子标记 SSR-X4 和 SSR-X25 界定的区间内,遗传距离约为 0.6cM,物理距离约为 190kb。该区间含有候选基因 *OsCCD8* (Os01g0746400),它是 *MAX4/RMS1/DAD1* 的同源基因,即 *D10*。因为 JHCA 和 XJC 与 *d10* 突变体的表型极其相似,暗示着 *xmd(t)*与 *d10* 可能是等位基因。*D10* 是抑制分枝的新型植物激素独角金内酯(strigolactone, SL)合成途径中的关键基因。外源施用 SL 的人工类似物 GR24 可恢复 XJC 的突变表型,结合 *D10* 基因的测序分析结果,进一步证实了 *XMD(t)*就是 *D10* 的等位基因。携带 *d10/xmd(t)*基因的多蘖矮秆突变体 JHCA 和 XJC 是 SL-缺失突变体,是研究水稻分蘖分子机理的理想材料。

抑制分枝的 SL 或其衍生物作为一种新激素被发现是当前植物生物学领域的一项重大突破,植物分枝抑制的 *MAX/RMS/D* 途径是当前的研究热点。虽然该途径中的一些关键基因已被陆续克隆出,但其抑制分枝的信号调控机制的细节尚不清楚。为了在蛋白质组水平揭示 SL 对水稻分蘖抑制的分子机理,本研究运用蛋白质组学技术分析了 *d10/xmd(t)*突变体 XJC 响应 GR24 处理的差异表达蛋白和磷酸化蛋白。

研究发现,GR24 抑制了黑暗中萌发和生长的 XJC 幼苗胚轴的伸长,这种对细胞分裂的抑制机理可能与之对分蘖芽生长的抑制相关。差异蛋白质组学分析法联用 MALDI-TOF 质谱分析鉴定出 9 个差异表达蛋白,其中蔗糖合成酶 2、核酮糖二磷酸羧化酶/加氧酶大亚基等 2 个蛋白表达上调,推定表达的 5-甲基四氢叶酸-高半胱氨酸 S-甲基转移酶、推定的晚期胚胎丰富蛋白、腺苷激酶、肌动蛋白-7 和胞质抗坏血酸过氧化物酶 2 等 5 个蛋白表达下调,假定蛋白 OsI\_09330 和线粒体磷转运蛋白等 2 个蛋白特异性消失。它们分别参与了碳代谢、能量代谢、防卫、蛋白质代谢和细胞骨架保持等功能途径。在对照蛋白质组中高丰度表达的线粒体磷转运蛋白的特异性消失

可能与 GR24 对的细胞分裂的抑制作用密切相关，它是根据质谱数据在拟南芥蛋白数据库中匹配到的同源蛋白，对于水稻蛋白质数据库而言，可能是个新蛋白。

蛋白质磷酸化是信号转导的重要机制。本研究利用特异性抗体检测并鉴定出 8 个响应 GR24 的磷酸化蛋白，包括 6 个丝氨酸磷酸化蛋白和 2 个苏氨酸磷酸化蛋白，这些蛋白为：推定的磷酸甘油酸激酶（胞质）、推定的磷酸丙糖异构酶、磷酸甘露糖变位酶、推定的还原酶、推定的顺乌头酸水合酶（胞质）、推定的氨基转移酶 AGD2、甲基丙二酸-半-醛脱氢酶和尿苷二磷酸葡萄糖焦磷酸化酶。它们分别表现出磷酸化、去磷酸化和磷酸化减弱等三种磷酸化状态的改变，表明它们可能是 SL 信号通路的组成成分。

本研究还运用蛋白质组遗传分析方法，寻找与引起多蘖矮秆突变表型的 *d10* 基因密切相关的蛋白质标记。发现佳禾丛矮（JHCA）与广陆矮 4 号（GLA4）的叶鞘、根系和基部节间蛋白质组中存在着丰富的多态性遗传标记，可分为三种类型，即：位移变异、“有/无”变异和表达量变异。以分蘖最重要的着生部位基部节间为对象，结合 F<sub>2</sub> 分离后代的突变型植株及其他野生型、突变型品种的分析，在基部节间蛋白质组中发现一个与多蘖矮秆性状共分离的“有/无”（P/A）变异型蛋白 B31，经质谱鉴定为推定表达的羟基-羟基磷酸酯磷酸基变位酶。它在突变型植株中皆表现为“无”，而在所有野生型植株中皆表现为“有”，推测其功能可能与水稻的分蘖抑制调控有关。本研究同时表明，基于 2-DE 的蛋白质组学遗传分析方法可成为水稻群体遗传学和表达基因组遗传作图的标记重要来源，并有利于相关基因靶蛋白的快速寻找。

**关键词：**水稻 多蘖矮秆 蛋白质组学

## Abstract

Rice is one of the most important crops. In rice, the tillering and plant height are two major agronomic traits affecting the plant architecture. In our genetic studies, a high-tillering dwarf indica rice, JHCA, was found to carry two nonallelic recessive genes, semidwarf gene *sd-1* and high-tillering dwarf gene *xmd(t)*. Through the segregation analysis, we realized that the *xmd(t)* gene was actually responsible for its high tillering and partially its severely dwarfing in JHCA. A strain line possessing *xmd(t)* singly was isolated from the hybrid offspring of JHCA and wild tall-culm variety GC13. After being inbreeding for several generations, it got up to genetic stability and was named XJC. By linkage analysis with molecular markers, the *xmd(t)* gene was fine mapped in the region between SSR-X4 and SSR-X25 on chromosome 1. The genetic distance and physical distance of this region were about 0.6cM and 190kb, respectively. This region contains *OsCCD8*(Os01g0746400), was the closest homolog of *MAX4/RMS1/DAD1*, and it was *D10* in fact. Because the phenotypical similarity among JHCA, XJC and *d10* mutant, it was suggested that *XMD(t)* might be *D10*. *D10* acts as an important member participating in the biosynthesis of strigolactone, a new class of phytohormones involved in inhibiting plant branching. The phenotypes of XJC could be rescued by supplementation with GR24, a synthetic strigolactone analog. Associating with the results of *D10* gene sequence analysis, these findings strongly supported the notion that *XMD(t)* was the allele of *D10*. JHCA and XJC are SL-deficient mutants, and they are suitable for the study of tillering molecular mechanism.

The discovery of strigolactone (SL) or its derivatives as a new phytohormone that inhibiting shoot branching was a recent significant breakthrough in plant biology, and *MAX/RMS/D* pathway of plant branching control is the current hot point. Though several key genes had been cloned, how SL signaling regulating the control of branching remains unclear. To reveal the molecular mechanism of rice tillering controlled by SL at the proteome level, we performed a proteomics study of SL-regulated proteins and phosphoproteins in *d10/xmd(t)* mutant XJC.

Strigolactone inhibited mesocotyl elongation in mutant XJC during germination and growth in darkness. The negatively regulative mechanism in inhibiting mesocotyl cell division in rice might be related strongly to the negative regulation in axillary bud, which might explain the observations that high-tillering of the *d* mutants is enhanced. Nine SL-responsive proteins were identified by differential proteomic analysis and MALDI-TOF-MS. Sucrose synthase 2 and ribulose biphosphate carboxylase large chain were up-regulated by SL, whereas 5-methyltetrahydropteroyltriglutamate-homocysteine

methyltransferase (putative, expressed), putative late embryogenesis abundant protein, putative adenosine kinase, actin-7 and L-ascorbate peroxidase 2 (cytosolic) were down-regulated. Hypothetical protein OsI\_09330 and mitochondrial phosphate translocator were newly-disappeared specially. The main functions of these proteins were carbohydrate metabolism, energy, defense, protein metabolism and cytoskeleton maintenance. The special disappearance of mitochondrial phosphate translocator with high expression in control might be tightly related to the inhibitory effect of GR24 on cell division. This protein was matched in the *Arabidopsis* proteins bank by its PMF data. It might be a new found protein to rice proteins bank.

Protein phosphorylation has been recognized as an important mechanism for signaling. Six phosphoserine-containing proteins and two phosphothreonine-containing proteins were identified by special phosphoantibody. They are putative phosphoglycerate kinase (cytosolic), putative triosephosphate isomerase, phosphomannomutase, putative reductase, putative aconitate hydratase(cytoplasmic), putative aminotransferase AGD2, methylmalonate semi-aldehyde dehydrogenase and UDP-glucose pyrophosphorylase. Phosphorylation, de phosphorylation and weakeness of phosphorylation were observed in these proteins. The change of phosphorylation status suggested that they might act as important roles in the signal transduction.

Proteome genetic approach was applied to find the protein marker which relating closely to *D10*. With the genetic analysis of proteome, plentiful polymorphic genetic markers existing in the proteome of leaf sheaths, roots and basal nodes from JHCA and GLA4 were found. They can be divided into three types: (1) position shift variations (PSs), (2)presence/absence variations (P/As) and (3) variations in protein amount. Associating with the mutant plants in the F<sub>2</sub> segregative generation and other wild type varieties, a P/A type variation protein marker co-segregating with the high-tillering mutant phenotype was found from the basal nodes proteome, which was identified as carboxyvinyl-carboxyphosphonate phosphorylmutase (putative, expressed). It showed 'absence' variation in all mutant plants, whereas showed 'presence' in all wild type plants. The result suggested that this protein might be related to the inhibiting of tillering in rice. Our research showed that proteomic approach based on 2-DE can be an important source of markers for population genetics and mapping the expressed genome in rice, and act as a advantageous tool to find the target proteins of special gene.

Key words: Rice(*Oryza sativa* L. ), High-tillering dwarf, Proteomics

## Abbreviations

- ABA: Absciscic acid, 脱落酸
- ACN: Acetonitrile, 乙腈
- AP: Ammonium persulfate, 过硫酸氨
- 6-BA: 6-benzylaminopurine, 6-苄氨基嘌呤
- BAC: Bacterial artificial chromosome, 细菌人工染色体
- BR: Brassinosteroid, 油菜素内酯
- BSA: Bovine serum albumin, 牛血清白蛋白
- CCDs: Carotenoid cleavage dioxygenases, 类胡萝卜素裂解双加氧酶
- CDPK: Calcium-dependent protein kinases, 钙依赖蛋白激酶
- CPEP: carboxyvinyl-carboxyphosphonate, 羧基乙烯基-羧基磷酸酯
- CTK (或CK): Cytokinins, 细胞分裂素
- 2,4-D: 2,4-dichlorophenoxy acetic acid, 2,4-二氯苯氧乙酸
- 2-DE: Two-dimensional polyacrylamide gel electrophoresis, 二维聚丙烯酰胺凝胶电泳
- DTT: Dithiothreitol, 二硫苏糖醇
- EST: Expressed sequence tags, 表达序列标签
- GA: Gibberellin, 赤霉素
- IAA: Auxin, 生长素
- ICAT: Isotope-coded affinity tags, 同位素编码亲和标签技术
- IEF: Isoelectric focusing, 等电聚焦
- IPG: Immobilized pH gradient, 固相pH梯度
- ISSR: Inter-simple sequence repeat, 中间简单序列重复
- ITMI: International triticeae mapping population, 国际小麦族作图群体
- JA: Jasmonic acid, 茉莉酮酸
- MALDI-TOF MS:  
Matrix-assisted laser-desorption ionization-time of flight mass spectrometry,  
基质辅助激光解析电离飞行时间质谱
- MEP: 2-C-methyl-D-erythritol-4-phosphate, 2-甲基-赤藓糖醇磷酸
- MudPIT: Multidimensional protein identification technology, 多维蛋白鉴定技术
- Mr: Relative molecular mass, 相对分子质量
- P/A: Presence/absence variation, 有/无变异



PAGE: Polyacrylamide gel electrophoresis, 聚丙烯酰胺凝胶电泳

PEP: phosphoenolpyruvate, 磷酸烯醇式丙酮酸

PEPM: phosphoenolpyruvate mutase, 磷酸烯醇式丙酮酸变位酶

pI: Isoelectric point, 等电点

PMF: Peptide mass fingerprinting, 肽质量指纹图谱

PQL: Protein quantity locus, 蛋白质数量位点

PS: Position shift variation, 位移变异

QTL: Quantitative trait locus, 数量性状基因座

RAPD: Random amplified polymorphic DNA, 随机扩增多态性DNA

RFLP: Restriction fragment length polymorphism, 限制性片段长度多态性

RubisCO: Ribulose-1,5-bisphosphate carboxylase/oxygenase,  
核酮糖-1, 5-二磷酸羧化酶/加氧酶

SA: Salicylic acid, 水杨酸

SAR: Systemic acquired resistance, 系统获得性抗性

Ser: Serine, 丝氨酸

SDS: Sodium dodecyl sulfate 十二烷基硫酸钠

SL: Strigolactone, 独角金内酯

SSR: Simple sequence repeat, 简单序列重复

TEMED: N,N,N',N'-Tetramethylethylenediamine, N,N,N',N'-四甲基二乙胺

TFA: Trifluoroacetic acid, 三氟乙酸

Thr: Threonine, 苏氨酸

Tyr: Tyrosine, 酪氨酸

M: Mole, 摩尔

mM: Millimole, 毫摩尔

$\mu$ M: Micromole, 微摩尔

l: Litre, 升

ml: Millilitre, 毫升

$\mu$ l: Microlitre, 微升

d: Day, 天

h: Hour, 小时

min: Minute, 分钟

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## 第一章 文献综述

水稻是世界上最重要的粮食作物之一,如何进一步提高水稻产量来满足人类不断增长的需求已成为现代农业生产上的一项主要任务。分蘖和株高是水稻株型结构中两个最重要的农艺性状,株高关系到水稻的抗倒性和耐肥性,而分蘖直接决定水稻的穗数并进而影响水稻的产量。在水稻矮化育种的基础上,合适的分蘖能力一直是水稻理想株型育种的一个主要目标。因此,揭示水稻分蘖的分子调控机理,对于培育株型合理、成穗率高、单穗重的超级水稻品种具有重大的现实意义。

分蘖是单子叶植物的一种特殊的分枝现象。已有的研究表明,单子叶植物与双子叶植物在分枝抑制调控途径具有保守性<sup>[1-3]</sup>。高等植物通过株高、分枝决定和分枝角度等的不同呈现出不同的植株形态,长期以来,植物株型形成的分子遗传基础一直是发育生物学的研究热点。近年来,人们通过对模式植物拟南芥、番茄以及单子叶植物水稻和玉米等相关突变体的筛选及相关基因的克隆鉴定,已对植物株型形成的分子基础有了较深入的了解<sup>[4]</sup>。随着一系列重要基因的克隆,植物分枝发育调控机制的研究正逐渐成为作物分子育种的重要依据。

### 1.1 水稻矮秆突变体研究

发生于 20 世纪 50 年代至 60 年代初的矮化育种是中国水稻育种史上一个重要的里程碑,在国际水稻研究上也是一个巨大的成就。因此,水稻矮秆突变体对水稻遗传育种具有重要意义。从广义上讲,水稻的矮生性是指成熟期水稻株高比正常植株缩短的遗传特性。同时,根据株高缩短的程度,又可将广义的矮秆分成半矮秆、矮秆和极矮秆三种类型<sup>[5]</sup>。狭义的矮秆通常指成熟时植株高度等于或低于原正常植株高度一半的矮秆突变系;半矮秆则是指株高介于矮秆和正常高度之间的类型。科学家对矮秆的遗传基础进行了广泛的研究。日本水稻基因连锁群和命名委员会将矮秆基因及少数半矮秆基因统一以 *d* 为符号,根据矮秆基因被鉴定的时间顺序,已从 *d1* 到 *d61*,其中缺 *d8*、*d15*、*d16*、*d25*、*d34*、*d36*,共 55 个矮秆基因<sup>[6]</sup>。半矮秆基因定名为 *sd* 系统,目前已报道的有 15 个,其中 *sd1* 基因是水稻生产利用中主要的半矮秆基因,被誉为“绿色革命”基因<sup>[7]</sup>。水稻经常发生矮秆变异,在育种实践中具有良好利用价值的矮



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